Coevolution of male and female mate choice can destabilize reproductive isolation

Thomas G. Aubier[1,2,3,*], Hanna Kokko[3] & Mathieu Joron[1,*]

1. Centre d'Ecologie Fonctionnelle et Evolutive, CEFE - UMR 5175 - CNRS, Université de Montpellier, EPHE, Université Paul Valéry, 1919 route de Mende, F-34293, Montpellier 5, France

2. Institut de Systématique, Evolution, Biodiversité, ISYEB - UMR 7205 - CNRS, MNHN, UPMC, EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités, 57 rue Cuvier, CP50, F-75005, Paris, France

3. Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057, Zurich, Switzerland

∗ Corresponding authors; e-mail: thomas.aubier@normalesup.org; mathieu.joron@cefe.cnrs.fr

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Abstract

Sexual interactions play an important role in the evolution of reproductive isolation, with important consequences for speciation. Theoretical studies have focused on the evolution of mate preferences in each sex separately. However, mounting empirical evidence suggests that premating isolation often involves mutual mate choice. Here, using a population genetic model, we investigate how female and male mate choice co-evolve (phenotype matching rule) and how this affects reproductive isolation. We show that the evolution of female preferences increases the mating success of males showing reciprocal preferences, favouring mutual mate choice. However, the evolution of male preferences weakens indirect selection on female preferences and, with weak genetic drift, the coevolution of female and male mate choice leads to periodic episodes of random mating with increased hybridization rate ('preference cycling'). Thus, counterintuitively, the process of establishing premating isolation proves very fragile if both sexes can contribute to assortative mating.

INTRODUCTION

Reproductive isolation among taxa can be caused by many different isolating barriers, such as ecological divergence, premating isolation, hybrid sterility and microspatial partitioning[1,2]. While those barriers have been well described, their temporal stability is little studied either theoretically or empirically. Yet, if the barriers that isolate diverged populations are not stable, the consequent recurring hybridization may have profound consequences for species evolution (e.g., speciation[3], transgressive segregation[4], adaptive introgression[5], genetic swamping[6]).

Assortative mating – the tendency of individuals of similar phenotype to mate together more often than expected by chance – is widespread in animals[7] and plays a key role in generating premating reproductive isolation[8]. Assortative mating can arise as a by-product of adaptive divergence via temporal or spatial isolation[9], or can be driven by various behavioural processes[10]. Of particular interest is the case of homotypic mate preferences ('matching mating rule'[11]), where individuals preferentially choose mates with which they share phenotypic traits such as colours[12,13] or acoustic signals[14]. When mate choice is based on phenotypic traits under disruptive selection, choosy individuals with homotypic mate preferences are less likely to produce offspring with unfit intermediate phenotype.

Theoretically, indirect selection favours increased choosiness (i.e., strong homotypic preferences), which establishes premating isolation between diverging populations[11,15–20]. Additionally, choosiness induces positive frequency-dependent sexual selection that favours the most common phenotype; if mating success varies among individuals and assortment is not perfect, individuals matching the most common phenotype have the highest mating success. If the population is already differentiated, choosiness therefore induces additional disruptive selection on the phenotypic trait used as the basis of mate choice; this can drive further evolution of choosiness in sympatry[21–23] (but note that this sexual selection pressure can also inhibit the evolution of strong choosiness in sympatry[22–24] or parapatry[25–27]). Empirically, homotypic preferences based on such "magic traits" subject to disruptive selection are often associated with premating reproductive isolation during speciation in the presence of gene flow[25,28,29]. Here, we are interested in whether this isolating barrier is stable when choosiness can be expressed by both sexes.

Theoretical developments have focused on the evolution of choosiness in each sex separately[15–20,30,31]. As explained above, indirect selection favours increased choosiness in females and in males. Nevertheless, evolutionary pressures acting on female and male choosiness are profoundly different. Under strict polygyny, males can be thought of as an unlimited resource for females and all females have therefore equal mating success[32]. Females, on the other hand, often represent a limited resource for males, with male-male competition for access to females generating differential male mating success. Consequently, having a preference directly affects how much competition a male faces in gaining a mate. Typically, males place themselves in a disadvantageous competitive setting if they preferentially court "popular" females – which can be phrased as sexual selection acting directly against male preferences[30,33,34].

The extent of courtship effort (resources[35,36] or time[37]) allocated towards preferred females is another key, but underappreciated, factor in the evolution of male mate choice. Male preferences can only evolve if the lack of mating with unpreferred females improves mating opportunities with preferred ones. Typically this is conceptualized as reallocation of courtship effort, and male mate choice is hampered if complete reallocation is difficult to achieve. Male preferences can nevertheless evolve if direct or indirect benefits (e.g., increased probability to mate[33,38], fertility[33,39], or offspring quality[30,40]) outweigh these costs. Previous theoretical studies have shown that male choosiness can evolve by reinforcement[30]

and that strategic male courtship allocation can generate polymorphic male preferences[31], ultimately causing reproductive isolation between populations. Overall, however, female choosiness, which does not associate with competitive and opportunity costs, is considered more likely to evolve than male choosiness[30].

In some interspecific sexual interactions, both males and females discriminate against heterospecifics, and therefore engage in mutual mate choice with respect to species identity[41–44]. In cichlid fishes[45,46] and *Heliconius* butterflies[2,13,47–49], which are text-book examples of potential speciation via premating isolation, both males and females can display homotypic preferences based on colour. However, the consequences of mutual mate preferences for reproductive isolation remain to be explored. Preferences have been shown to evolve independently if female and male choices are based on distinct traits[33]. However, females and males with mutual homotypic preferences often use the same trait to evaluate potential mates. Choosiness in one sex therefore influences the evolution of choosiness in the other through a genetic linkage disequilibrium[33,50–53]. Female choosiness may also strongly favour the evolution of male choosiness by directly increasing the mating success of choosy males focusing their courtship effort on females that are likely to accept them as mates.

Here, by analyzing a population genetic model, we characterize the coevolutionary dynamics of female and male mate choice based on the same phenotypic trait under disruptive selection. We then assess its effects on the stability of reproductive isolation. We show that female choosiness favours the evolution of male choosiness and that selection for mutual mate choice should be common. In turn, because female and male preferences are based on the same phenotypic trait, male choosiness weakens indirect selection on female choosiness. In finite populations, this causes coevolutionary dynamics of 'preference cycling', initiated by drift and completed by selection, that strongly destabilize reproductive isolation.

MODEL OVERVIEW

We model the evolution of assortative mating in sympatry, based on three diploid biallelic loci that segregate independently (no physical linkage). Disruptive viability selection acts on an ecological locus A, but ecological divergence is hampered under random mating that brings divergent ecotypes (AA and aa) together to hybridize. Additionally, we implement two distinct choosiness loci F and M that are independently expressed in females and in males, respectively. Both sexes can therefore use the trait under disruptive viability selection as a basis for mate choice ('one-allele mechanism'[54] using a matching rule). Female and male choosiness are ecologically neutral, but they can experience indirect selection via linkage disequilibrium with the ecological locus. Hybridization rates between ecotypes may decline due to assortative mating caused either by female, male or mutual preferences. Unless stated otherwise, we assume that the alleles coding for choosiness are recessive (only FF females and MM males are choosy).

Each generation, disruptive viability selection first occurs with strength s, such that heterozygotes at the ecological locus (Aa) suffer viability costs. Males then court females and are 'visible' to them (i.e., available as potential mates) proportionally to the courtship effort they invest. Choosy males (MM) prefer to court females that match their own ecological trait. In case of a mismatch, they reduce their courtship effort to a very small fraction $\epsilon_{\mathrm{m}} << 1$ of what nonchoosy males would invest. The courtship effort thus saved can be reallocated towards preferred females, where the extent of this reallocation is described by the parameter α. In particular, if choosy males reallocate all saved courtship effort towards preferred females ($\alpha = 1$), they enjoy a strong mating advantage over nonchoosy males with these particular females. Females also express different propensities to accept courting males. Choosy females (FF) prefer males that match their own ecological trait. We assume that, in case of a mismatch, they reduce the probability of mating to a very small value $\epsilon_{\mathrm{f}} << 1$. Small ϵ_{f} and ϵ_{m} therefore reflect strong choosiness. Unlike males, all females have the same mating success (polygyny). The theoretical genotype frequencies in the next generation are the result of the frequencies of mating among genotypes, with the new generation formed assuming Mendelian inheritance of all loci with no physical linkage.

This three-locus diploid model involving mutual mate choice is too complex to produce analytical solutions[33]. The behaviour of the model can be assessed, however, by numerical analyses and computer simulations. We first analyze the deterministic behaviour of the model, assuming an infinite population. Subsequently, we then perform stochastic simulations in populations of finite, yet appreciable, size to account for genetic drift affecting traits under weak selection. Each generation, stochasticity is introduced by sampling K offspring individuals following the distribution of genotype frequencies predicted by the deterministic model (just like in the Wright-Fisher model of genetic drift). Additionally, in those stochastic simulations, we assume that alleles can mutate in offspring.

DETAILED METHODS

Genotypes

Our population genetic model is based on three autosomal diploid loci. Alternative alleles at each locus are represented by small and capital letters. An ecological locus, A, is subject to disruptive selection and can be used as a basis for mate choice (phenotypic matching). Additional loci F and M alter female and male choosiness (i.e., strengths of homotypic preference) before mating. We assume that choosiness alleles code for either no choosiness or strong choosiness, i.e., preferences vary from indiscriminate to almost fully assortative. We assume no physical linkage (i.e., loci are on different chromosomes or very far apart on the same chromosome) and alleles assort independently of one another in gametes following Mendel's second law. This simplifying assumption allows us to reduce the number of dynamic variables of our genetic system. There are three genotypes per locus (e.g., AA, Aa and aa for the A locus), and, therefore, we track the frequencies of $3^3 = 27$ genotypes in the population.

Deterministic simulations

Assuming discrete generations, we follow the evolution of genotype frequencies $\mathbf{p}(t)$ within an infinite population over time. $\mathbf{p} = \{p_i\}$ is a vector consisting of 27 elements $\{p_1, p_2, ..., p_{27}\}$ referring to the frequencies of the 27 genotypes present in newborn offspring. The life cycle is as follow:

(1) Disruptive viability selection on the ecological locus

Environmental/ecological pressures act on an adaptive ecological trait and favours sympatric divergence into two distinct ecotypes occupying niches of equal size. In that sense, parameter $s' > 0$ confers an advantage to the rarer of the two homozygotes AA and aa, ensuring the maintenance of polymorphism. We also assume that heterozygotes Aa suffer viability costs with parameter s representing the strength of disruptive viability selection on locus A. Following these assumptions, the genotype frequencies after viability selection are:

$$p_i^{\mathrm{S}} = \begin{cases} p_i \left(1 + s' \left(0.5 - \frac{\sum_{k \in \mathrm{aa}} p_k}{\sum_{k \in \mathrm{aa} \cup \mathrm{AA}} p_k}\right)\right) \Big/ \hat{N}, & \text{if } i \in \mathrm{aa} \\ p_i \left(1 + s' \left(0.5 - \frac{\sum_{k \in \mathrm{AA}} p_k}{\sum_{k \in \mathrm{aa} \cup \mathrm{AA}} p_k}\right)\right) \Big/ \hat{N}, & \text{if } i \in \mathrm{AA} \\ p_i \left(1 - s\right) \Big/ \hat{N}, & \text{if } i \in \mathrm{Aa} \end{cases} \quad (1)$$

The normalization factor $\hat{N}$ ensures that the genotype frequencies p_i^{S} sum up to 1. If $s' = 0$, the ecological allele that is more frequent initially may outcompete the other allele ('gene swamping'[55]) via positive frequency-dependent sexual selection induced by female choosiness, hampering divergence[21,56,57]. To prevent fixation of a single ecological genotype, we always set $s' > 0$ (leading to $p_{AA}^{\mathrm{S}} \approx p_{aa}^{\mathrm{S}}$).

(2) Male choice and courtship

$P_{m,f}^{\male}$ denotes the courtship effort of a male with genotype m towards females with genotype f (m and $f \in \{1, 2, .., 27\}$). Males with genotype mm or Mm at locus M are nonchoosy and court all females with the same intensity ($P_{m,f}^{\male} = 1$ towards

all females). Homozygous MM males are choosy (i.e., they express homotypic preferences), and their courtship depends on the match between the ecological trait (locus A) of the female and their own. In case of a mismatch (e.g., between a male with genotype AA and a female with genotype Aa or aa), choosy males reduce their courtship effort to a small fraction $P^{\male}_{m,f} = \epsilon_{\mathrm{m}} << 1$ (small ϵ_{m} thus reflects strong choosiness). In other words, choosy males reduce resources (e.g., time or energy) spent on courting unpreferred females. Saved courtship effort can be reallocated (totally, partially, or not at all) towards courtship of preferred (matching) females. The extent of this reallocation is described by parameter α. Overall, of all possible courtship events that could happen in the population, a fraction $C_{m,f}$ will occur between males of genotype m and females of genotype f:

$$C_{m,f} = p^{\mathrm{S}}_m \, p^{\mathrm{S}}_f \overbrace{\left(\overbrace{P^{\male}_{m,f}}^{\substack{\text{Baseline courtship effort of a male of genotype } m \text{ towards a female of genotype } f}} + \overbrace{\alpha \left(1 - \sum_{f'=1}^{27} p^{\mathrm{S}}_{f'} P^{\male}_{m,f'} \right)}^{\substack{\text{Courtship effort that a male of genotype } m \text{ reallocates}}} \times \overbrace{\frac{P^{\male}_{m,f}}{\sum_{f'=1}^{27} p^{\mathrm{S}}_{f'} P^{\male}_{m,f'}}}^{\substack{\text{Proportion of courtship effort that a male of genotype } m \text{ reallocates towards a female of genotype } f}} \right)}^{\text{Total courtship effort of a male of genotype } m \text{ towards a female of genotype } f} \quad (2)$$

where p^{S}_m and p^{S}_f are the frequencies of males of genotype m and females of genotype f after viability selection. If $\alpha = 1$, choosy males reallocate all saved courtship effort towards preferred females and therefore enjoy a strong mating advantage over their competitors with these particular females. Contrary to previous models [30,33,38,58], however, male preferences can induce lost courtship opportunities. If $\alpha < 1$, only part of saved courtship effort is reallocated ($\sum_m \sum_f C_{m,f} < 1$) and total courtship effort may differ between individual males ($\sum_f C_{m,f} \neq p^{\mathrm{S}}_m$). Equation (2) therefore differs from those previous models and is instead analogous to a model of female mating preferences with opportunity costs [23].

(3) Female choice and mating

We assume that males are 'visible' to females (i.e., available as potential mates) proportionally to their courtship effort, defining a baseline mating rate which can then be adjusted downwards or upwards by female choice. $P^{\female}_{f,m}$ denotes the willingness of a female with genotype f to mate with males with genotype m. Females with genotype ff or Ff at the locus F mate indiscriminately ($P^{\female}_{f,m} = 1$ with all males), leading to mating rates that are directly proportional to courtship efforts. Homozygous FF females are choosy (i.e., they express homotypic preferences). Their decision to mate depends on the match between the ecological trait of the male and their own. In case of a mismatch, choosy females reduce the probability of mating to a small fraction $P^{\female}_{f,m} = \epsilon_{\mathrm{f}} << 1$ of the baseline (small ϵ_{f} reflects strong choosiness). Thus, the overall proportion of matings $M_{m,f}$ that occur between males of genotype m and females of genotype f is given by:

$$M_{m,f} = \frac{C_{m,f} P^{\female}_{f,m}}{\sum_{m'=1}^{27} C_{m',f} P^{\female}_{f,m'}} \times p^{\mathrm{S}}_f \quad (3)$$

This equation is analog to previous population-genetics models of mating with female preferences [25,30,32,33,38,58]. It ensures that all females, even the ones that are less preferred by males, have the same mating success (no cost of

choosiness). Likewise, the mating success of females with and without a preference is equal ($\sum_m M_{m,f} = p_f^{\mathrm{S}}$). These assumptions are realistic for a polygynous mating system; relaxing them by implementing a cost of female choosiness ($\sum_m M_{m,f} < p_f^{\mathrm{S}}$ for $f \in$ FF) does not change our conclusions (Appendix A).

(4) Zygote formation

Expected genotype frequencies $\mathbf{p}(t+1)$ of zygotes in the next generation is calculated by summing the appropriate mating frequencies $M_{m,f}$, assuming Mendelian segregation and free recombination between all loci.

Stochastic simulations

Based on the above deterministic model, we also perform stochastic simulations in finite populations to account for drift at loci under weak selection. To do so, for each generation, we first apply equations (1) to (3) to the vector $\mathbf{p}(t)$, yielding to the expected frequency distribution of genotypes in generation $t+1$. The new vector $\mathbf{p}(t+1)$ is then obtained by randomly sampling K offspring individuals from this distribution. Additionally, we assume that each allele of each offspring mutates to the alternative allele with probability μ.

Parameters and initialization

Unless stated otherwise, we perform simulations with strong choosiness associated to genotypes FF and MM ($\epsilon_{\mathrm{f}} = 0.01$, $\epsilon_{\mathrm{m}} = 0.01$). We also set $s' = 0.5$ to ensure that polymorphism at the ecological locus A is maintained. Simulations start with only alleles f and m present in the population. Once the population has reached ecological equilibrium, 1% of choosy males and females are introduced such that choosiness alleles are in linkage equilibrium with the ecological locus.

Deterministic equilibrium is typically reached in less than 1,000 generations. In stochastic simulations, we model populations of appreciable size $K = 500$ with a probability of mutation $\mu = 10^{-3}$ per individual and per locus. For each combination of parameters tested, 40 stochastic simulations were run for 100,000 generations and statistics were calculated by averaging over these runs.

Note that we do not consider the case where sexual selection induced by female preferences hampers ecological divergence[21–23]. In our model, if heterozygotes Aa are initially in high frequency, positive frequency-dependent sexual selection on the A locus increases the mating success of those heterozygotes but does not increase their frequencies (crosses Aa×Aa, Aa×AA, Aa×aa all lead to 50% Aa offspring). Therefore, sexual selection does not inhibit ecological divergence.

RESULTS

Viability and sexual selection on female and male choosiness

Viability and sexual selection may act directly on ecological or choosiness loci (through differential viability and male mating success among genotypes, respectively; see Fig. S1), and, despite free recombination, also generate linkage disequilibrium between loci by creating statistical non-random associations between alleles (Fig. S2). In particular, the majority of choosy females and choosy males are homozygous at the ecological locus. Additionally, choosy males often carry alleles coding for female choosiness (which are neutral during courtship). This linkage disequilibrium between choosiness loci arises because choosy females and choosy males both use the same ecological trait as the basis of mate choice and, therefore, tend to mate with each other. Via this linkage disequilibrium, selection changing frequencies at a given locus will also change frequencies at other loci. As detailed below, such indirect selection plays a key role for the evolution of male and female choosiness.

To understand the intricate interplay of selective forces, we first consider cases where choosiness can evolve in only one sex. Disruptive viability selection directly acts on the ecological locus (black arrow, Fig. 1) with homozygotes having high viability (hereafter, 'homozygous' and 'heterozygous' refer to the genotype at the ecological locus). Female choosiness can also induce positive frequency-dependent sexual selection on the ecological locus (green arrow, Fig. 1), such that males that are homozygous at the ecological locus have the highest mating success. Consequently, in the case where only female choosiness can evolve, female choosiness is favoured by indirect viability and sexual selection due to linkage disequilibrium with the ecological locus (Fig. 1a and S3).

The situation is rather different if only male choosiness can evolve. Unlike female choosiness, male choosiness does not induce direct sexual selection on the ecological locus, because females in our idealized polygyny scenario do not differ in their mating success, even if some receive less courtship than others. However, male choosiness intensifies male-male competition for the preferred female type, which induces sexual selection on the male choosiness locus itself (pink arrow, Fig. 1). Because the majority of choosy males are homozygous at the ecological locus (linkage disequilibrium), males courting 'popular' homozygous females face strong competition for mating opportunities (Fig. S1). Choosy homozygous males therefore place themselves in a disadvantageous competitive setting and have low mating success. Additionally, if reallocation of courtship effort is only partial ($\alpha < 1$), choosy males lose courtship opportunities, which lowers their mating success (blue arrow, Fig. 1). Consequently, in the case where only male choosiness can evolve, male choosiness is favoured if negative sexual selection is offset by indirect viability selection due to linkage disequilibrium with the ecological locus (Fig. 1b and S3).

We now turn to our main case, where choosiness can evolve in both sexes. In addition to selection acting on female and male choosiness separately (Fig. 1a-b), choosiness in each sex now induces selective forces on choosiness in the opposite sex. First, because choosy females mainly reject nonchoosy (nonmatching) males, female choosiness directly increases the mating success of choosy males (red arrow, Fig. 1c). Second, sexual selection induced by female choosiness on the ecological locus also indirectly favours male choosiness (dashed green arrow, Fig. 1c). Finally, due to the linkage disequilibrium between choosiness loci, all selective forces acting on male choosiness affect indirectly the evolution of female choosiness and vice-versa (dashed pink, red and blue arrows in Fig. 1c).

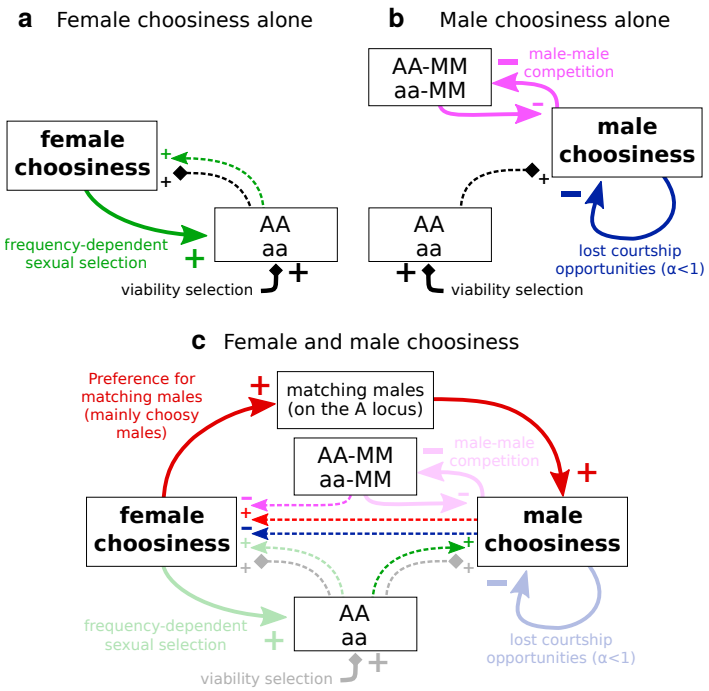

Figure 1: Selective forces acting on female and male choosiness if choosiness can only evolve in one sex (a, b) or in both sexes (c). Diamond arrows and classic arrows represent viability and sexual selection, respectively. Viability selection acts through differential survival (i.e., change in frequencies during the disruptive viability selection process), whereas sexual selection acts through differential male mating success (detailed in Fig. S1). Bold and dashed arrows represent direct and indirect selection, respectively. AA and aa refer to homozygotes at the ecological locus and MM to choosy males. Selective forces represented with a low opacity in subfigure c are the ones already shown in subfigures a and b.

To characterize the resulting coevolutionary dynamics of female and male choosiness, we measured the change in frequencies of choosy females and choosy males resulting from viability and sexual selection over one generation (Fig 2b-f). Interestingly, for $\alpha > 0$, the evolution of female choosiness changes the direction of sexual selection acting on male choosiness (change from sex. - to sex. + on male choosiness as the frequency of choosy females increases, Fig. 2c-f) and can even enforce the evolution of male choosiness (Fig. 2c and S3). Male choosiness can likewise change the direction of sexual selection acting on female choosiness, but in an opposite direction (change from sex. + to sex. - on female choosiness as the frequency of choosy males increases, Fig. 2b-f); male choosiness clearly inhibits the evolution of female choosiness if viability selection is weak (Fig. 2e-f and S3).

Note that indirect sexual selection acting on female choosiness does not necessarily reflect sexual selection acting on male choosiness (e.g., sex. - on female choosiness that overlap with sex. + on male choosiness in Fig. 2d-f), as indirect selection results from a three-locus linkage disequilibrium (between locus coding for the ecological trait, female choosiness and male choosiness). In particular, choosy males carrying alleles coding for female choosiness are largely homozygous at the ecological locus (Fig. S2). While choosy heterozygous males benefit from reduced male-male competition (contributing to sex. + on male choosiness), homozygous choosy males carrying alleles coding for female choosiness experience intensified male-male competition (strongly contributing to sex. - on female choosiness). As a whole, sexual selection can favour male choosiness (sex. +) and inhibit female choosiness (sex. -).

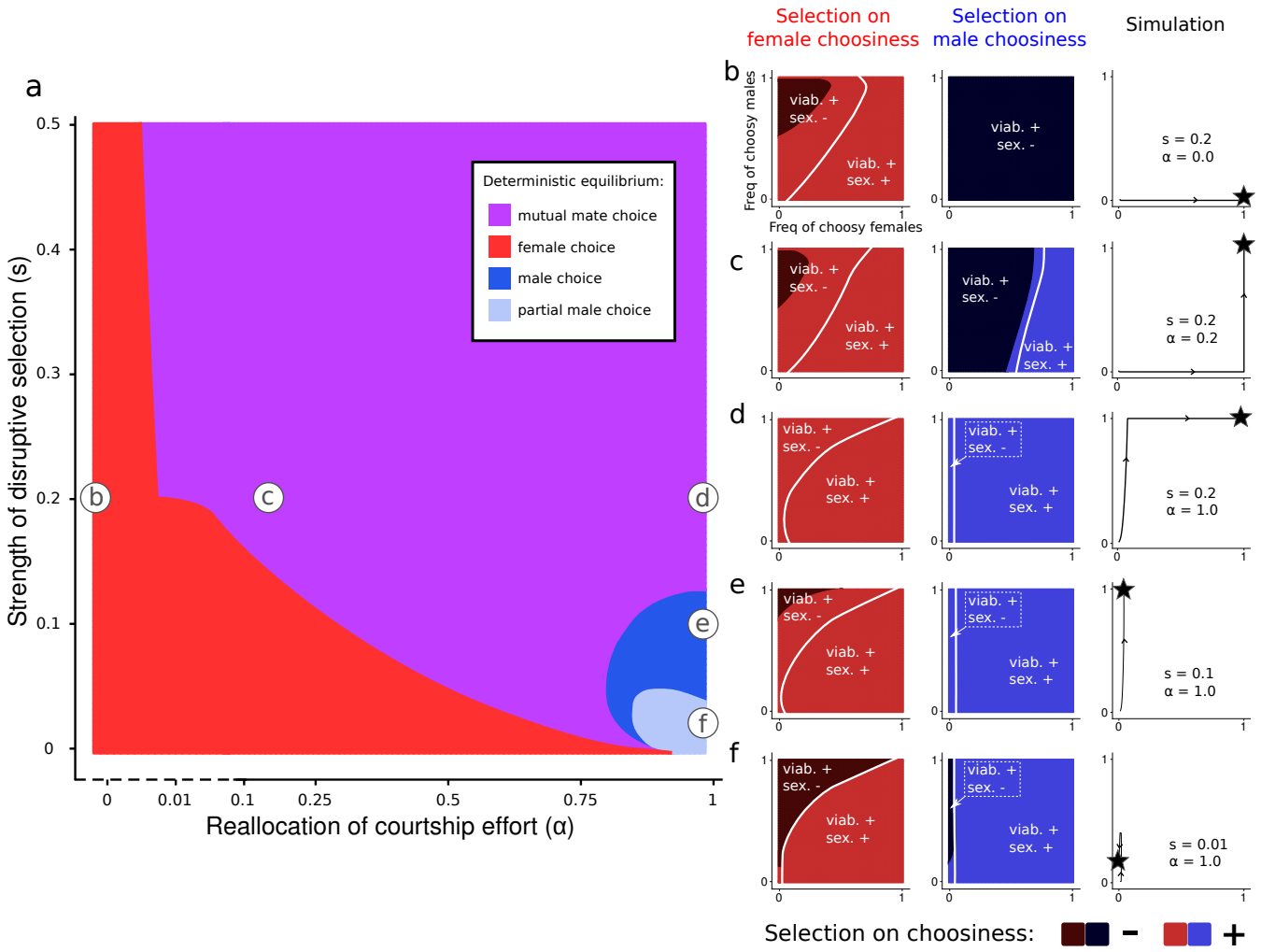

Figure 2: Deterministic equilibrium for different combinations of courtship reallocation (α) and strength of disruptive viability selection (s). Subfigures b-f refer to specific combinations of (α, s) marked in subfigure a. In the right-most plot of subfigures b-f, we draw the trajectory of individual simulations leading to deterministic equilibrium (represented by black stars, and colour-coded in subfigure a). To understand the direction of viability and sexual selection on female and male choosiness, we also measure the change in frequencies of choosy females and choosy males over one generation (in the red and blue plots, respectively). Viability selection (always positive, viab. +) is measured by the change in frequency before mating, and sexual selection (sex. - and sex. +, separated by the white line) by the change in frequency after mating. Dark and light colours indicate the overall frequency change due to the combined action of all selective forces (dark: decrease, light: increase). Note that sexual selection directly acts on male choosiness. In addition, sexual and viability selection act indirectly on both female and male choosiness via linkage disequilibrium between loci. Depending on (α, s), female mate choice, male mate choice or mutual mate choice can be the stable deterministic equilibrium (a). In particular, under strong disruptive viability selection ($s \geq 0.2$), mutual mate choice evolves even if choosy males reallocate little courtship effort towards preferred females ($\alpha \geq 0.01$, note the logarithmic scale in the left part of the α axis). In that case, the evolution of female choosiness favours the evolution of male choosiness by increasing the mating success of choosy males (sex. + in c).

Finally, if males are choosy, females avoid producing unfit hybrids regardless of their own choosiness, as males focus their efforts on matching females. This weakens the linkage disequilibrium between the female choosiness locus and the ecological locus (Fig. S2), and reduces indirect selection favouring female choosiness (cf. selection gradients in Fig 4), with the consequence that female choosiness may easily drift in finite populations. The implication of such weak selection for choosiness coevolution is assessed later using stochastic simulations.

Deterministic outcome: selection favouring mutual mate choice is common

If viability selection is weak, four different choosiness regimes can evolve at deterministic equilibrium depending on the extent of reallocation of courtship effort ($s < 0.05$, Fig. 2a). In particular, without reallocation of courtship effort ($\alpha = 0$), only female choosiness evolves by indirect viability and sexual selection. On the contrary, with complete reallocation of courtship effort ($\alpha = 1$), sexual selection acting on male choosiness can indirectly inhibit the evolution of female choosiness (Fig. 2e-f); in this case, assortative mating is caused only by complete or partial male choosiness (depending on the relative strength of viability and sexual selection, see Fig. S3). Note that this outcome is not reached if females are initially choosy.

If viability selection is strong, mutual mate choice is a common deterministic equilibrium ($s > 0.15$, Fig. 2a). It evolves even if choosy males reallocate very little of their courtship effort towards preferred females (for $\alpha \geq 0.01$ if $s \geq 0.2$). As explained above, female choosiness favours male choosiness by changing the direction of sexual selection (Fig. 2c). Recall that, while choosy individuals avoid courting/mating across ecotype boundaries, premating isolation is not complete ($\epsilon_{\mathrm{m}} \neq 0$ and $\epsilon_{\mathrm{f}} \neq 0$). Consequently, with mutual mate choice, female and male choosiness act in synergy to reduce hybridization rate between ecotypes (Fig. S4). Note that changing the dominance hierarchy of choosiness alleles does not change our results qualitatively (Fig. S5).

Stochastic simulations: coevolution of male and female mate choice increases hybridization rate

We next run stochastic simulations to investigate the coevolutionary dynamics of male and female choosiness in populations of finite, yet appreciable, size ($K = 500$). Unless stated otherwise, we here consider scenarios with strong disruptive selection ($s = 0.2$). We define a frequency threshold ($= 0.85$) above which female or male populations are considered to be mainly choosy (i.e., mainly express a choosy behaviour before mating). We thereby characterize four regimes of choosiness: female choice only ($\mathcal{F}$), male choice only ($\mathcal{M}$), mutual choice ($\mathcal{FM}$) and partial choice (i.e., both female and male populations are only partly choosy, $\mathcal{P}$) (Fig. 3a). Note that regime $\mathcal{P}$ includes the regime of complete random mating and is therefore different from the deterministic equilibrium of partial male choice described above (Fig. 2a).

The regime of choosiness can evolve away from mutual mate choice, leading to "preference cycling". – For $\alpha > 0.01$, our deterministic analysis predicts a stable equilibrium of mutual mate choice, yet with drift, choosiness traits can temporarily evolve away from this equilibrium (Fig. 3b), entering the regimes of male choice only (regime $\mathcal{M}$) or partial choice (regime $\mathcal{P}$). This is caused by drift-induced and selection-driven coevolutionary dynamics of female and male choosiness that we describe below.

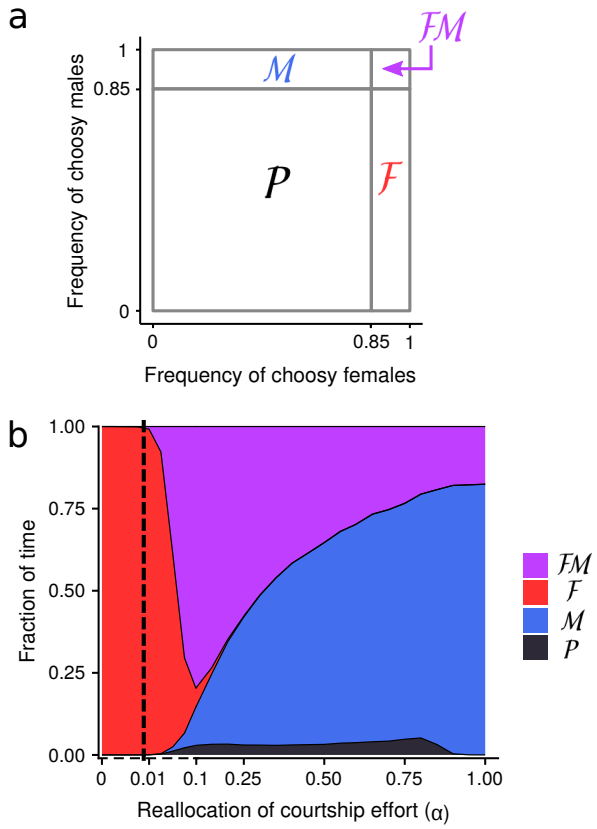

Figure 3: (a) Four regimes of choosiness are defined to describe stochastic simulations: mutual mate choice ($\mathcal{FM}$), male mate choice ($\mathcal{M}$), female mate choice ($\mathcal{F}$) and partial mate choice (i.e., both female and male choosiness occur at intermediate or low frequencies < 0.85, $\mathcal{P}$). (b) Fractions of time spent in each regime as a function of the reallocation of courtship effort α, in stochastic simulations with $s = 0.2$ and $K = 500$ measured once the equilibrium predicted by the deterministic model is reached for the first time. The vertical dashed line corresponds to the threshold above which the deterministic equilibrium is mutual mate choice ($\alpha > 0.01$, Fig. 2a). In that condition, however, assortative mating is often caused by male choosiness only (regime $\mathcal{M}$). Moreover, for partial reallocation of courtship effort ($\alpha \in [0.01, 0.9]$), female and male populations are partly choosy (regime $\mathcal{P}$) for significant time periods (5% of total time).

Despite selection favouring mutual mate choice, assortative mating is often caused solely by male choosiness (regime $\mathcal{M}$, Fig. 3b). When females are choosy, male choosiness is strongly favoured, with drift playing an insignificant role. However, when males are choosy, selection favouring female choosiness is weak (as explained above); the frequency of choosy females may now decrease through drift (Fig. 4). Nonchoosy females can persist for significant periods of time, during which assortative mating is maintained by male choosiness only (regime $\mathcal{M}$).

Female and male populations are rarely simultaneously partly choosy (regime $\mathcal{P}$) for extreme values of α (Fig. 3b). When $\alpha < 0.01$, selection favouring female choosiness is strong enough to keep female choosiness at high frequency, and the same applies for male choosiness when $\alpha > 0.9$. The situation changes at intermediate α values, for which female and male populations are partly choosy (regime $\mathcal{P}$) for significant periods of time (5% of time). Since male choosiness is favoured only when the frequency of choosy females is high, drift of female choosiness changes the direction of selection on

male choosiness, which can then lead to a regime of partial choosiness (regime $\mathcal{P}$, Fig. 4b-d). Although selection predicts a return to mutual mate choice (i.e., regime $\mathcal{P}$ is only transient), the process takes time, and an observed outcome at a particular point in time features large fractions of both females and males being nonchoosy (regime $\mathcal{P}$). Hereafter, 'preference cycling' refers to this coevolutionary dynamics of female and male choosiness going through deterministic cycles triggered by stochasticity, involving departure from regime $\mathcal{FM}$ into regimes $\mathcal{M}$, $\mathcal{P}$ and sometimes $\mathcal{F}$ (before returning to regime $\mathcal{FM}$). Preference cycling also occurs if we relax the hypothesis of polygyny (i.e., if we add a weak cost of female choosiness, Appendix A) or if we implement continuous choosiness traits (Appendix B).

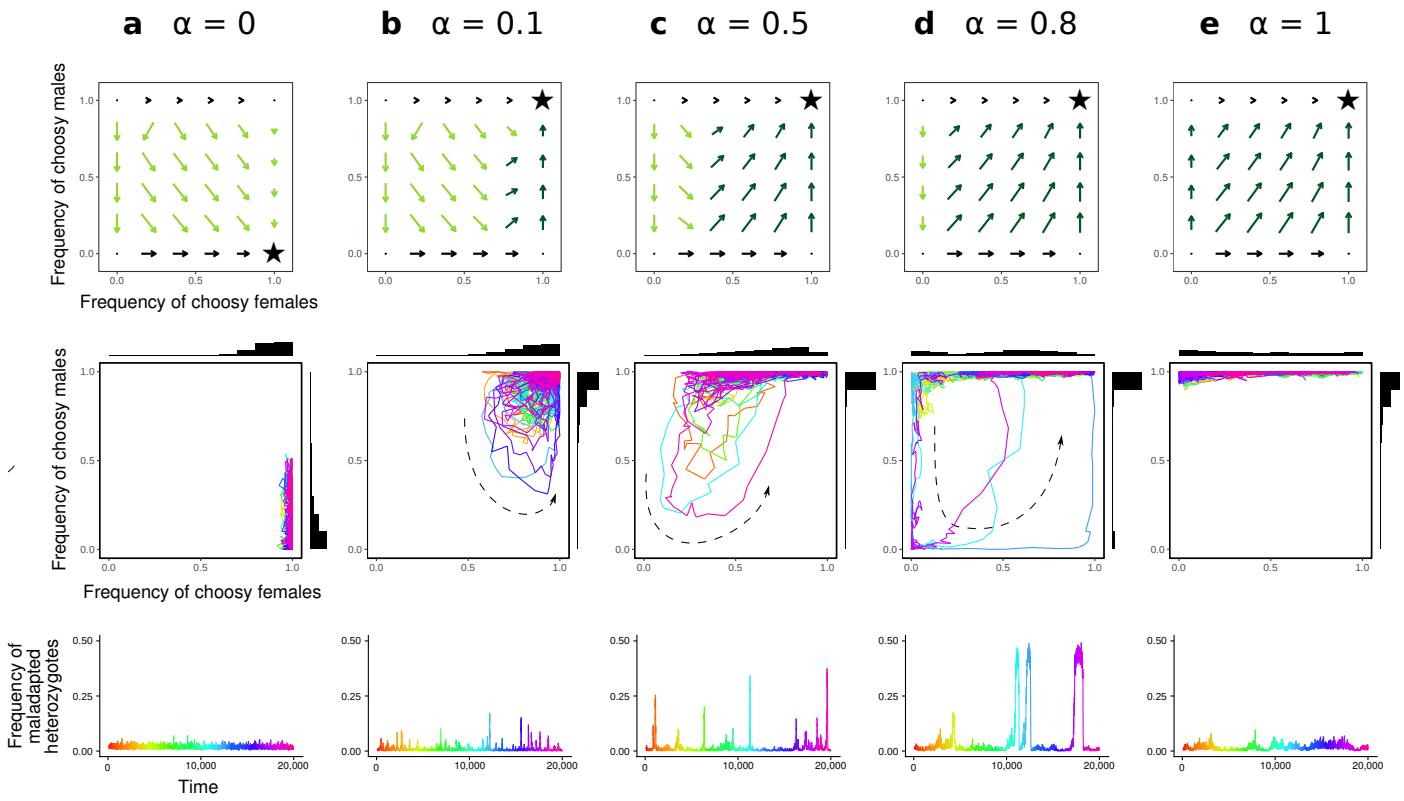

Figure 4: Selection gradients for female and male choosiness and examples of stochastic simulations ($s = 0.2$, $K = 500$) with different courtship reallocation values (α). From top to bottom, we represent the deterministic selection gradients for female and male choosiness, the evolutionary dynamics of choosiness and the resulting frequencies of maladapted heterozygotes at the ecological locus before viability selection (from the same simulations). The selection gradients for choosiness correspond to the relative change in frequencies of choosy vs. nonchoosy females and males over one generation (dark green arrows represent selection favouring male choosiness). Those representations of selection gradients are therefore simpler than in Fig. 2b-f. To highlight weak selection on choosiness, we here use a logarithmic scale to draw arrow vectors. Stars corresponds to the regimes of choosiness at deterministic equilibrium. The graphs in the second and third rows show stochastic simulations, started at the choosiness regime predicted by the deterministic analysis, and rainbow colour gradients correspond to the passage of time. Note that, in b-d, the stochastic simulations do not converge to the deterministic equilibrium, but instead display preference cycling, which direction is represented by a dashed arrow.

Consequences for reproductive isolation. – Since neither sex is assumed to ever achieve perfect choosiness ($\epsilon_m \neq 0$ and $\epsilon_f \neq 0$), it is not surprising that hybridization rate is the lowest in the regime of mutual mate choice ($\mathcal{FM}$), and that hybridization becomes somewhat more frequent during drift-induced excursions into the male choice regime ($\mathcal{M}$) (blue area in Fig. 5d). More importantly, hybridization strongly increases during deterministic excursions into the partial choice regime ($\mathcal{P}$) (grey area in Fig. 5d). The greatest increase in hybridization occurs if the population stays in this regime $\mathcal{P}$ for extended periods of time. As shown in Fig. 5, while the regime $\mathcal{P}$ is reached most frequently for $\alpha \simeq 0.1$, the average time spent in this regime is maximal for $\alpha \simeq 0.8$, and during these episodes, maladapted heterozygotes reach frequencies of up to 35%. Overall, preference cycling leads to temporary peaks of hybridization, which periodically homogenize populations (e.g., fluctuation of the F_{ST}, Fig. S6). In other words, even though mutual mate choice, whenever it occurs, achieves stronger assortative mating in the context of premating reproductive isolation, mate choice in its mutual form is particularly prone to periodical break-downs that, as a whole, hamper the maintenance of premating isolation. Notably, this is not the case when choosiness is favoured in one sex only (Fig. S7 and S8).

If disruptive viability selection is weak or population size is small, drift remains strong relative to indirect selection acting on female choosiness, and preference cycling occurs more frequently, increasing the overall hybridization rate (low s, Fig. S9; low K, Fig. S10). If alleles coding for choosiness are dominant instead of recessive, the complete fixation of the male choosiness allele occurs less often, and preference cycling induced by drift of female choosiness consequently occurs rarely (Fig. S11). Likewise, if male choosiness is sufficiently imperfect, preference cycling occurs less frequently, and the overall hybridization rate is decreased (high $\epsilon_m = 0.03$ instead of 0.01 in Fig. S12 and S13). This somewhat counterintuitive result is explained by the fact that, with imperfect male choosiness, selection on female choosiness never becomes so weak as to be overwhelmed by drift. More generally, preference cycling may occur if choosiness leads to a nearly perfect reproductive isolation among ecotypes – e.g., if premating isolation caused by choosiness is nearly perfect *per se* (Fig. S12 and S13) or if other barriers contribute to reproductive isolation in addition to premating isolation (Fig. S14). Under those conditions, which seem conducive to strong isolation among ecotypes, we show that coevolution of male and female choosiness strongly destabilizes reproductive isolation and increases hybridization rate.

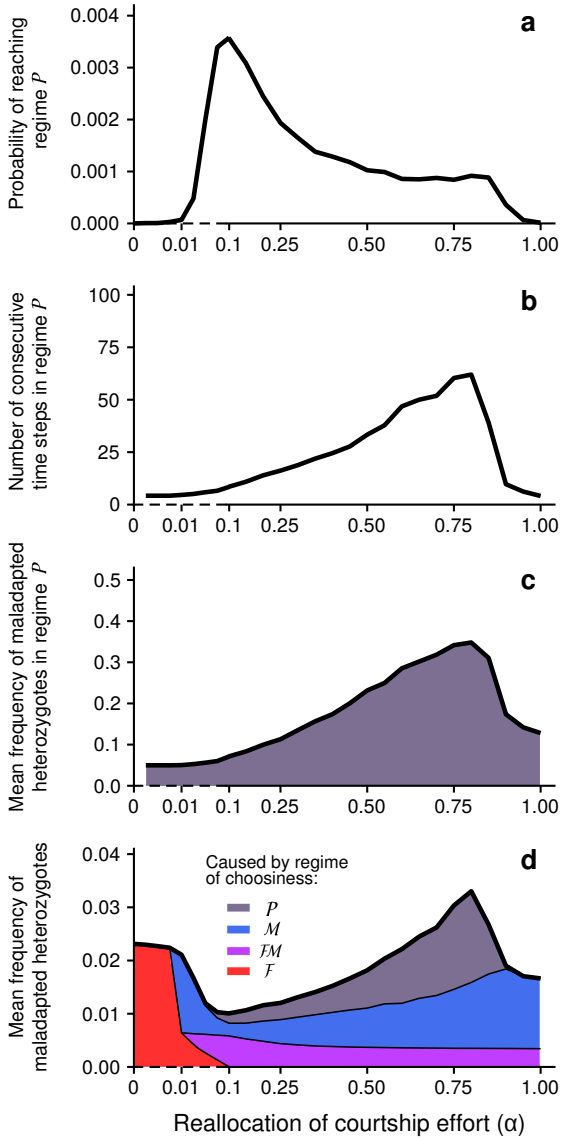

Figure 5: Coevolutionary dynamics of choosiness ('preference cycling') and resulting hybridization rate in stochastic simulations ($s = 0.2$, $K = 500$). To describe the coevolutionary dynamics of female and male choosiness, we record the mean probability of reaching regime $\mathcal{P}$ from regime $\mathcal{FM}$ or $\mathcal{M}$ (a), the mean number of consecutive time steps in regime $\mathcal{P}$ (b) and the mean frequency of maladapted heterozygotes (Aa at locus A) in regime $\mathcal{P}$ before viability selection (c) as a function of the reallocation of courtship effort (α). To assess the resulting hybridization rate, we record the mean frequency of maladapted heterozygotes over evolutionary time (d). In subfigure d, we also represent the mean contribution of each regime of choosiness to hybridization. In stochastic simulations, hybridization rate is increased by the coevolutionary dynamics of female and male choosiness despite selection favouring mutual mate choice (when $\alpha > 0.01$) (d). In particular, the coevolution of female and male choosiness leads to periodic episodes of random mating, strongly increasing hybridization rate (with up to 35% of hybridization in regime $\mathcal{P}$) (c).

DISCUSSION

Surprising coevolutionary dynamics of male and female mate choice occur when the preferences of both sexes are based on the same phenotypic trait under disruptive selection. We showed that choosiness in one sex influences the evolution of choosiness in the other, a factor that has not been considered in previous models of mate choice in the context of reproductive isolation [15–20,30,31]. Based on the predictions of our model, genetic drift, incomplete reallocation of courtship effort and strength of choosiness all prove to be important when understanding the outcome of this coevolutionary dynamics in terms of reproductive isolation.

In our model, male and female preferences are based on the same phenotypic trait, but are themselves governed by different loci. This genetic basis gives scope for preference coevolution. Selection generates linkage disequilibrium between preference and ecological loci (despite free recombination), and indirect viability and sexual selection resulting from this linkage disequilibrium has profound consequences for the evolution of choosiness in both sexes. In particular, female and male mate choice can substitute each other as drivers of assortative mating, but have different consequences on selection experienced by the opposite sex. Consider assortative mating where males are choosy while females are not. Male choosiness relaxes indirect selection on female choosiness, because all females avoid producing unfit hybrids when males focus their efforts on females of their own ecotype. Now consider assortative mating based on female choosiness; this changes selection on male choosiness in a different manner. Although female choosiness relaxes indirect selection on male choosiness, it also strongly favours the evolution of male choosiness through direct sexual selection. Male choosiness is a poor strategy when females are not choosy, as choosy males focusing on a subset of females place themselves in a disadvantageous competitive setting [30] and may incur opportunity costs. This changes if females are choosy: now choosy males have a high mating success, i.e. by disproportionately courting those females that are likely to accept them.

Female choosiness therefore favours the evolution of male choosiness if at least some of the courtship effort saved by refraining from courting unpreferred females can be reallocated to gain a mating advantage with preferred females. Under disruptive viability selection, male mate choice evolves more easily than without preference coevolution (i.e., in models investigating the evolution of choosiness in each sex separately [30]). Mutual mate choice is often favoured, resulting in strong reproductive isolation in infinite populations.

In finite populations, however, this regime of mutual mate choice is particularly unstable. With weak genetic drift, the coevolutionary dynamics of female and male mate preferences can lead to transient but periodic break-downs of premating isolation, strongly increasing hybridization rate. The fact that either sex can cause assortative mating makes it difficult for mutual mate choice to be maintained; more precisely, if male preferences are sufficiently strong to establish assortativeness, female choosiness has little effect on the mating outcome and is therefore free to drift. When female choosiness is reduced, selection against male choosiness is re-established, leading temporarily to a regime of random mating. This coevolutionary dynamic of 'preference cycling', initiated by drift and completed by selection, strongly destabilizes reproductive isolation and leads to periods of increased hybridization, which homogenize populations.

The establishment of premating isolation is often considered to be the first step towards speciation and its stability is therefore a key component for other isolating barriers to evolve. For instance, only stable premating isolation leads to the accumulation of genetic incompatibilities among taxa and to subsequent postzygotic isolation [59,60]. If selection favouring mutual mate choice induces preference cycling and dynamic instability of premating isolation, our results suggest it can

become an obstacle to speciation. This scenario contrasts with the traditional view of speciation as a gradual process characterized by a constant accumulation of barriers to gene flow ('speciation continuum')[2,61–63]. Speciation can also be "undone"; like assortative mating in our model, barriers to gene flow can dissolve and genetic discontinuities may vanish, thereby merging two taxa into a single population by hybridization[64,65]. Our model predicts such cycles of divergence and gene flow may actually characterize the process of diversification in nature.

Empirical research often estimates isolating barriers between pairs of populations varying in their level of differentiation to track the so-called 'speciation continuum'[2,61]. Yet, it is important to remember that such measures, being snapshot measurements in time, do not yield information on the long-term stability of reproductive isolation. Our predictions regarding the coevolutionary dynamics of male and female mate preferences means that premating isolation caused by mutual mate choice should be interpreted cautiously: whether gene flow is reduced over long periods of time is an open question. If a species range is partially fragmented, preference cycling could also cause variation in the degree of reproductive isolation among local populations, as observed, for instance, in *Catostomus* fish species[66,67]. Yet, variation in hybridization is rarely quantified across several natural populations, and our study highlights the usefulness of studies characterizing the strength of isolating barriers at a broader spatial and temporal scale.

The coevolutionary dynamics of female and male mate preference (and resulting reproductive isolation) depends crucially on how much courtship effort males can reallocate towards preferred females, as a result of foregoing courting unpreferred females. By considering the reallocation of courtship effort (α), our model covers a wide variety of courtship and mating systems in animals. In particular, "courtship effort" may refer to time (e.g., for mate searching or performing complex displays[37]) or energy (e.g., for resources-demanding spermatophores[35] or nuptial gifts[36]). Additionally, foregoing certain courtship opportunities and searching for more preferred mates might entail mortality costs, affecting the extent of reallocation of courtship effort. Therefore, to understand the process of divergence between taxa, it is important to obtain estimates of how much courtship effort choosy males can reallocate in nature. Based on our predictions, selection should favour mutual mate choice even with little reallocation; otherwise male choice should be deleterious. However, if reallocation is only partial, preference cycling may occur, possibly limiting divergence.

The extent and stability of reproductive isolation also depends on how accurately existing preferences can be expressed. Imperfect preference may occur for many reasons. For instance, in *Heliconius melpomene* and *Heliconius cydno*, female and male preference loci are associated with different colour pattern loci[49]. Therefore, individuals may not completely stop courting/mating across ecotype boundaries because each sex may rely on different aspects of the phenotype. Our model predicts this error-proneness could strengthen selection favouring mutual mate choice, which could in turn inhibit preference cycling and stabilize reproductive isolation. Thus, perhaps counterintuitively, our model suggests that imperfect male preferences lead to strong reproductive isolation in the long term by maintaining selection favouring female preferences, preventing drift-induced preference cycling. Such counterintuitive results are not unheard of: in the context of local adaptation, imperfect female choice has been shown to be more strongly favoured by selection than perfect choice because it maintains a higher diversity of male types in the population[68]. Likewise, many theoretical studies have found cases where sexual selection favours partial choosiness[22–25]. Our study adds to this quest the possibility of preference cycling in situations where choosiness evolves as a quantitative trait (see Appendix B). In particular, if choosiness only evolves to a partial degree, preference cycling may not occur; counterintuitively, this may "favour" speciation.

Our predictions are not limited to the context of emerging reproductive isolation among diverging populations in

sympatry. We can expect similar coevolutionary dynamics of female and male preferences in more advanced stages of reproductive isolation, e.g. after secondary contact. Indeed, disruptive viability selection may be caused by genetic incompatibilities among more distantly related taxa. In that context, preference cycling could also temporally increase hybridization rate and, conceivably, explain the formation of 'hybrid swarms' and subsequent genetic introgression [5] or hybrid speciation [69].

Overall, our theoretical model adds support to the idea that premating isolation may often be readily reversible [26,60,70]. Intriguingly, we show that premating isolation should be particularly unstable when selection favours mutual mate choice. We highlighted some factors that could inhibit preference cycling (strong selection against hybrid, high carrying capacity, imperfect choices, extensive reallocation of courtship efforts). The geographical context of speciation and more detailed look into alternative genetic architectures (e.g., 'two-allele mechanisms' [54], physical linkage among choosiness loci) could conceivably change the modalities of preference cycling and should therefore be investigated in future theoretical studies. It will also be fruitful to consider preference cycling in a system with potentially multiple isolating barriers, for if the time between episodes of hybridization during preference cycling is very long, other isolating barriers might have time to evolve despite preference coevolution taking place. On the empirical side, the occurrence of preference cycling and its impact on reproductive isolation remains to be tested. More generally, our study should stimulate further research on the stability of barriers to gene flow.

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